

# Chapter 1

## An Introduction to South American Wetland Forests: Distribution, Definitions and General Characterization

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**Abstract** This chapter provides an introduction to the ecology of wetland forests, their ecophysiology, distribution, species diversity, classification and use, with emphasis on Amazonia. Wetland forests occur in all continents and all regions except in deserts, high altitudes, and high latitudes. Their importance for humans and the environment is often underestimated because in developed or densely colonized regions such as Europe, North America, Australia, and the Indian sub-continent, many of them have already been destroyed or strongly modified. In other regions, such as Siberia, the Zaire River basin and the Amazon River basin they still

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cover large areas; however, scientists and politicians have placed little emphasis on their study and protection, or on developing sustainable management practices. In this chapter, we describe the general terminology for wetland forests and provide a classification of Amazonian wetland forests. We discuss the distribution of major wetland forests in South America and the impact of hydrology and nutrient status of water and soils. Distribution, species diversity, and the level of adaptation of trees of wetland forests is the result of long periods of evolution, without major extinction episodes. These conditions prevailed for many millions of years in the Amazon basin as shown by paleo-climatic and paleo-botanical evidence, leading to the development of the most species rich and highly adapted floodplain forest on the globe. In light of this history, we give examples for specific adaptations and survival strategies. Finally, Amazonian wetlands have been colonized by humans since their arrival on the sub-continent, about 12,000 years BP. More recently, European immigrants have used the wetlands for fishing, subsistence agriculture, timber exploitation and increasingly for cattle and water-buffalo ranching. Large scale ranching activities are especially detrimental for the forested Amazonian wetlands, because ranchers destroy wetland forests to increase the area of natural and planted pastures. This is also detrimental for forestry, fisheries, and the maintenance of biodiversity.

## 1.1 Introduction

Formerly, wetland forests were common in most parts of the continents, except in deserts, high latitudes, and high altitudes. Human hunters and gatherers quickly discovered that wetlands provided water, game animals, and protection and used them despite their negative aspects, such as insect nuisance and flooding. When humans became sessile, they recognized the great potential of river floodplains for agriculture and ranching because of their fertile soils. This was especially true for large tropical river floodplains with a predictable flood pulse. Accordingly, high cultures developed, for instance, along the Euphrates and Tigris Rivers in Mesopotamia, the Ganges, and Brahmaputra Rivers in India, and along the Nile River in Egypt. In the floodplain of the lower Amazon River, traces of human colonization date back about 12,000 years BP (Roosevelt 1999). Humans adjusted their management methods to natural flood cycles and were able to benefit from them.

In temperate regions, unpredictable floods initially hindered colonization of the floodplains. However, with increasing technical knowledge, dike construction improved and floodplains became increasingly used for traditional upland agriculture or for cattle ranching during low-water periods. These activities and the increasing demand for wood resulted in an accelerated destruction of floodplain forests in nearly all countries. The demand for arable land to accommodate an increasing population also led to the drainage of swamps and the destruction of swamp forests. Today, wetland forests belong to the most threatened forest types worldwide. Human pressure on remaining forest plots is rising directly due to logging for timber

and firewood, agriculture, pasture formation, housing and infrastructure construction, or indirectly due to hydrological changes, such as water abstraction, diking, and flooding by reservoir construction, all of which negatively impact forest habitats.

These activities are not limited to densely populated areas but also increasingly affect wetlands in remote areas (Junk 2002). The Amazon River basin harbors a human population of about 25 million people, of which about 70% live in urban centers. The human population density in large areas is <0.5 person per square kilometer. Despite this low density, the floodplain forests along the large Amazonian Rivers are becoming severely affected by logging and by transformation to crop land and pasture for cattle ranching (Goulding et al. 1996; Ohly 2000a,b; Junk and Piedade 2005).

Scientific research on Amazonian wetlands started at the beginning of the last century (summarized in Junk and Piedade 2004). Botanists were fascinated by the species-rich forests able to survive floods up to 10 m deep for as long as up to 8 months per year. The first floristic studies were carried out by Spruce (1908), Huber (1910), and Ducke (1913), and later by Ducke (1949), Ducke and Black (1953), Rodrigues (1961), and Takeuchi (1962), among others. These studies revealed different forest types and identified flooding, the nutrient status of water and sediments, and phytogeography as factors influencing the diversity of species composition and distribution.

At the beginning of the 1970s, the Brazilian government initiated major efforts to link the economically underdeveloped Amazon basin to the industrialized southern region of the country. Large projects for the construction of highways and airports, hydroelectric energy production, mining, petrol exploitation, agriculture, cattle ranching, and timber exploitation, and the establishment of a free-trade zone at Manaus stimulated a scale of development that could not be accompanied or controlled adequately by administrative or legislative measures and, even less, guided by scientific research. Research concentrated mostly on priorities financed by the government and was thus forced to ignore other important fields. Negative consequences of the development projects on the wetlands and their resources, especially floodplain forests, were thus inevitable.

The valiant efforts of a Brazilian scientist, Dr. Marcio Ayres, resulted in the targeting of floodplains for environmental protection. In 1983, Ayres, who was a doctoral student at the time, went to the Mamirauá region, near Tefé, to study the white-uacari monkey (*Cacajao calvus calvus*), which is endemic to that area. He wrote an excellent thesis on the monkey and its habitat, the floodplain forest of Mamirauá (Ayres 1986, 1993). Moreover, he also alerted the Brazilian Environmental Agency and the government of the State of Amazonas to the need to protect the area. This resulted in the establishment, in 1990, of the first Sustainable Management Reserve in Amazonia. Currently, the reserve protects about 1,124 million hectares of floodplain area most of it covered by near-pristine floodplain forest. This area constitutes an important platform for basic and applied research on different aspects of the central Amazonian floodplains and provides opportunities to practically test management options (Queiroz and Peralta 2010).

Along with many individual researchers, two teams realized long-term studies on Amazonian floodplain forests. At the beginning of the 1960s, Professor Harald

Sioli and co-workers together with scientists at the Instituto Nacional de Pesquisas da Amazonia (INPA) started ecological research on the Amazon floodplain near Manaus. Junk (1980) was the first to point out the flood pulse as the driving force in river floodplain systems and later published, with his colleagues Bayley and Sparks, the Flood Pulse Concept, which became an internationally recognized analysis of the processes in large-river floodplains (Junk et al. 1989). Research on the floodplain forest began in the 1980s (Worbes 1983) and was intensified in the mid-1990s with the financial assistance of the Brazilian Research Council (CNPq) and the German Ministry of Science and Technology (BMBF). The results of these studies are presented in the chapters of this book.

In the Peruvian pre-Andean Amazon basin, scientists from the University of Turku, Finland, started investigations in the early 1980s, in cooperation with several Peruvian institutions (Oficina Nacional de Evaluación de Recursos Naturales, ONERN, Instituto Nacional Geológico, Mineralógico y Metallúrgico, INGEMMET, Universidad Nacional de la Amazonia Peruana, UNAP, and others). The team concentrated on floristic studies, the description and mapping of forest types on floodplains and upland, and on relating these types to river dynamics and soil quality. It highlighted the importance of river activity and geologic dynamics in the pre-Andean region for plant species diversity in Amazonia (Kalliola et al. 1993).

In the following sections, we discuss the terminology used for wetland forests in general and for Amazonian wetland forests specifically. We review the actual distribution of wetlands in South America and the environmental factors affecting them. General information is provided on the evolution of Amazonian floodplain forests, the different types are characterized, and the various classification systems are discussed. We also describe the general strategies employed by trees to survive periodic flooding and the use of field measurements by researchers to estimate flood tolerance. Finally, services provided by floodplain forests to humans are discussed.

## 1.2 Terminology of Wetland Forests

The English scientific literature uses the general term “riparian forests” for wetland forest communities along rivers and lakes. There are many definitions of riparian wetlands. Hydrologically, they are defined as “lowland terrestrial ecotones which derive their high water tables and alluvial soils from drainage and erosion of adjacent uplands on the one side or from periodic flooding from aquatic ecosystems on the other” (McCormick 1979). A functional definition states that “riparian areas are three-dimensional ecotones of interaction that include terrestrial and aquatic ecosystems, that extend down to the ground water, up above the canopy, outward across the floodplain, up the near-slopes that drain to the water, laterally into the terrestrial ecosystem, and along the water course at a variable width” (Ilhardt et al. 2000).

Both definitions point to the ecotonal character of riparian wetlands between water bodies on the one side and the upland on the other. At their smallest scale, riparian wetlands can be the immediate water’s edge – where some aquatic plants and animals

form a distinct community – that becomes periodically flooded over areas of a few tens of meters in width. At medium scale, these wetlands comprise bands of vegetation, while at the largest scale they form extended floodplains, tens of kilometers in width, along large rivers. In the latter case, the complexity of the riparian wetlands increases to the extent that many scientists confer upon them the status of specific ecosystems (Junk 1980; Odum 1981; Mitsch and Gosselink 2000).

Riparian zones are covered by different plant communities, including different types of wetland forests. When riparian forests become extended, e.g., in floodplains along large rivers, such as the Mississippi River, the term “bottomland hardwood forest” is often used. The term “gallery forest” is frequently applied to riparian forests along water bodies in un-forested landscapes. Forests growing in swamp habitats with relatively stable water levels and long-lasting flood cycles are called swamp forests. These are dominated by a few highly flood-resistant species, such as the Bald Cypress (*Taxodium distichum*) and Water Tupelo (*Nyssa aquatica*) in North America, and palm trees in South America (*Mauritia* spp., *Astrocaryum* spp., and *Bactris* spp.). Forests in brackish water are called mangrove forests.

Here, we use the term “wetland forests” to refer to all types of forests subject to irregular, seasonal, or long-term flooding. “Floodplain forest” is used for all types of forests subject to periodic flooding by freshwater, and “swamp forest” for all types of forests subject to long-lasting flooding or waterlogging of the soil with freshwater. The term “riparian forest” is reserved for narrow forest strips along water bodies in forested and unforest landscapes, e.g., savannah areas (Rodrigues 2000).

Every region has local names that describe the different types of wetland forests. These names may provide insight into the type of flooding regime and the nutrient status of the system, or indicate dominant tree species. But local names are often used differently in different regions and therefore must be defined when used in the scientific literature. This is later shown for the terms *várzea* forest and *igapó* forest, which are used to describe the floodplain forest types that we studied in Central Amazonia. Non-wetland forests on the upland (*terra firme*) are called *terra firme* forests.

### 1.3 Occurrence of Wetland Forests in South America

Wetland forests occur all over South America because of the large number and vast extension of wetlands. A vegetation map of South America (Eva et al. 2002) based on multi-resolution satellite data indicated the areas listed in Table 1.1.

However, these numbers no doubt strongly underestimate the extent of wetlands, since only large wetlands were mapped and the definition of vegetation types remains biased in favor of terrestrial types that are better known. Junk (1993), using RADAM/BRASIL maps and botanical data on plant communities, estimated that 20–25% of Amazonia is periodically flooded. For all of South America, this number should amount to at least 15%, i.e., about three times the area indicated by Eva et al. (2002). The data reported by Melak and Hess (2010) confirmed the estimates of Junk (1993).

**Table 1.1** Extent of wetlands and water bodies of South America (Eva et al. 2002)

Type of wetland	Extent (km <sup>2</sup> )	Locality
Mangrove forests	17,290	East coast, from Orinoco delta down to Salvador West coast, down to Tumbes in Peru
Freshwater flooded forests	199,281	Along large Amazonian Rivers, Orinoco upper reaches of Rupununi and Mazaruni, coastal flooded forests from the delta of the Orinoco to the Maroni River, northern Amapá to the mouth of the Amazon River (west of the island of Marajó)
Swamp forests, open with palms	53,907	In Peru, the Pastaza fan; in Brazil, Amapá coast, western part of Marajó, and courses of the Guaporé River
Flooded savannah	320,941	Llanos of Venezuela/Colombia, northern parts of Rio Atrato and Rio Magdalena in Colombia, Campos de várzea along the Amazon River and its tributaries, Ilha do Bananal, Pantanal do Mato Grosso, parts of the Llanos of Moxos, west bank of Paraguay River, wet chaco, lower reaches of the La Plata River, south of the confluence of the Paraná and Paraguay Rivers
Flooded shrublands	12,957	Region north of the Rio Negro and along the Rio Branco in Roraima
Moorelands/heath	106,896	Mosaic of bogs, herbaceous and shrub vegetation in the humid temperate region in southern Chile and Argentina
Salt pans	9,409	Altiplano
Water bodies (natural & artificial)	220,219	
Total	940,900	

About half of the wetland area of Amazonia is covered by woody vegetation (Klinge et al. 1990). Hueck (1966) summarized what was known at the time about the ecology, species composition, and importance of the forests in South America. That study noted different wetland forests along the large South American rivers as well as rainwater-fed wetlands.

Most of the dense wetland forests are concentrated in the domain of the Amazon rain forest. They cover extended areas along the lower courses of all large Amazonian rivers (Klinge et al. 1990; Junk 1993) and the rivers of the southern Orinoco basin (Godoy et al. 1999; Rosales et al. 2001, 2002). Narrow strips of riparian forests also occur along all lowland rain forest streams. Large forested areas exist on insufficiently drained, periodically flooded white sand areas at the upper Negro and Orinoco River (Bana and Caatinga woodlands, Klinge et al. 1977; Klinge 1978b; Klinge and Medina 1979; Bongers et al. 1985). Prolonged flooding leads to species-poor *Mauritia flexuosa* palm swamps, e.g., north and south of the Negro River, upriver of the city of Barcelos, in the Amazon and Orinoco deltas, and in the pre-Andean zone. They are nutrient-poor and characterized by a small flood

amplitude. In Brazil, they are called *buritizal*, in Peru *aguajal*, and in Venezuela *morichal*. In Bolivia, southern Peru, and southwestern Brazilian Amazonia, there are bamboo swamp forests, which in Brazil are called *tabocal*.

Comprehensive studies on the geology, geomorphology, and vegetation cover of the pre-Andean zone showed a complex mosaic of habitats as a result of river activities; 26.6% of the lowland forests showed characteristics of recent erosional and depositional activity; 12% of the area comprised floodplains, and 14.6% previous floodplains with a mosaic of abandoned river beds, oxbows, and sedimentary beds of different age. These findings point to the overwhelming importance of rivers in structuring western Amazonia in recent history (Salo et al. 1986). Floristic studies identified floodplain forests of different species composition that are the result of recent river activity, different flooding regimes, or different water and soil qualities. The authors postulated that forest disturbances due to modern and previous river dynamics were partially responsible for the high biological diversity of the upper Amazon basin, and that the number of species confined to floodplain or denuded-soil forests is exceptionally high in the Amazon. Certainly, the close connectivity of upland forests and habitats to different flooding regime has favored the development of flood-resistant ecotypes of upland species (Kalliola et al. 1993).

Extended forests occur also in the large floodplain along the lower Paraguay-La Plata River. Large parts of the floodplain forests along the upper and middle Parana River have been destroyed because of the construction of hydroelectric power plants, which now occupy large areas of the former floodplain. Remnants can still be found in the 250-km-long stretch between the Porto Primavera Dam and the Itaipu Reservoir (Thomaz et al. 2004).

Large wetlands are found in savanna areas, such as the Pantanal at the upper Paraguay River, the Bananal at the Araguaia River, the Moxos Savannas at the Madre de Dios, Beni, Mamoré, and Guaporé Rivers in Bolivia, the Roraima and Rupununi Savannas in northern Brazil and the Guianas, and the Llanos of Venezuela. They are partially covered by different types of flood-tolerant forests and strips of riparian forests along river courses as well as around lakes, and savannah vegetation that at high water comprises many aquatic macrophytes (Junk 1983). Swamps along the headwaters of Brazilian cerrado streams covered mostly by sedges, grasses, herbaceous plants, and a few shrubs and trees are called *veredas*.

Permanent wet depressions are covered by palm swamps (*Mauritia flexuosa*). Along the courses of all rivers in the savanna, cerrado, and chaco areas, there are species-rich gallery forests. These forests occupy the ecotone between the dry upland and the river channel and form important forested corridors in the landscape that allow the migration of animals between isolated forest plots. They also represent important refuges for upland tree species that occur along their edges (Kellman et al. 1994; Meave and Kellman 1994; Meave et al. 1991).

Along the Atlantic Ocean coast, mangroves begin to grow in small patches from about 28°S to Central America, forming major forests near São Luis (5°S), in the Amazon River Delta, the Orinoco River Delta, and the Magdalena River Delta. At the coast of the Pacific Ocean, mangroves occur only in small patches and extend southerly only down to the Gulf of Guayaquil (5°S) (Lacerda et al. 2002).



## 1.4 The Impact of Hydrology on South American Wetlands

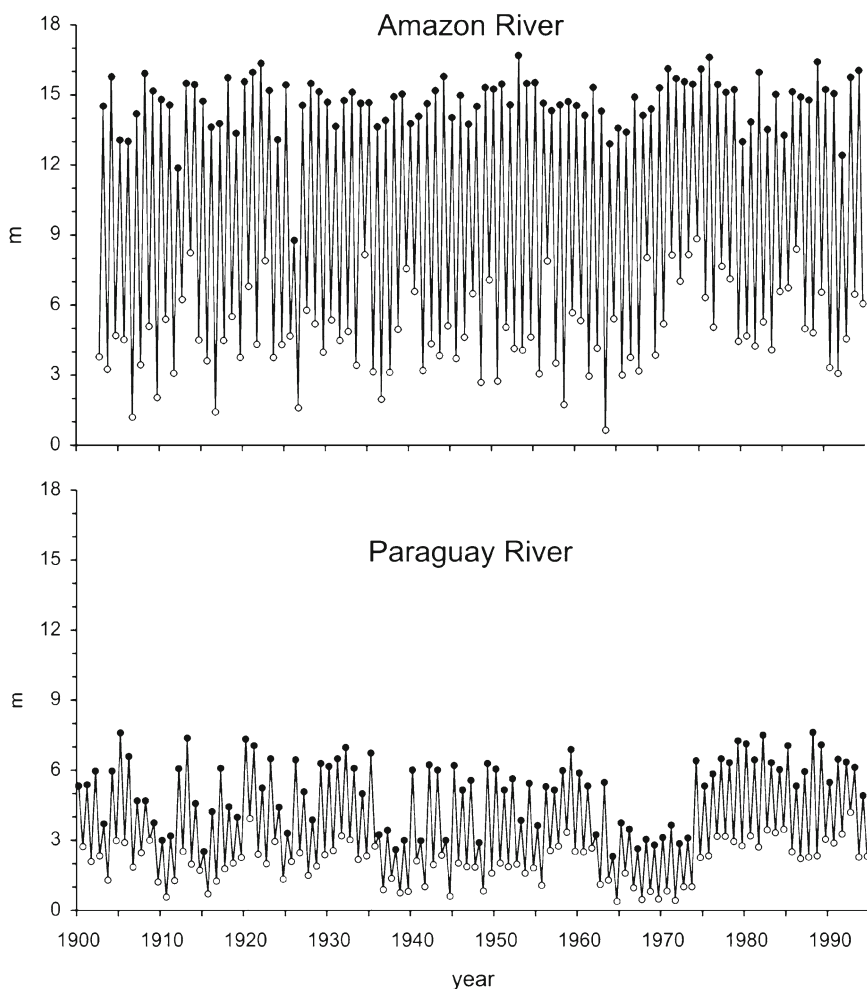
The conceptual basis to explain the importance of the length, depth, frequency, shape, and predictability of inundation on large-river floodplains in general was elaborated by Junk et al. (1989) in their Flood Pulse Concept (FPC), which describes the structures and processes in large-river floodplains. The FPC states that the flood pulse is the driving force in floodplain systems. It controls both the occurrence and the distribution of plants and animals, determines life-history traits, affects primary and secondary production, and influences decomposition and nutrient cycles in water and soils. The predictability of the flood pulse facilitates the adaptation of organisms to the change between aquatic and terrestrial phases, increasing their ability to efficiently make use of periodically available resources. In temperate regions the light/temperature (summer/winter) pulse, and in semiarid regions the precipitation (dry/rainy season) pulse may overlap with the flood pulse, obscuring the impact of the latter. For further discussions of the FPC, see Junk and Wantzen (2004) and Junk (2005).

Large Amazonian rivers integrate the individual precipitation events of large catchments, which, in turn, are influenced by pronounced dry and rainy seasons and by the snow melt in the Andes. Therefore, these rivers show long-lasting, predictable flood pulses of high amplitude (Fig. 1.1). The ecology of the Central Amazon River floodplain has been well-studied, for example, in Sioli (1984a,b), Junk (1997a), and Junk et al. (2000a). These studies described a predictable arrangement of plant communities that is controlled not only by the inundation stress of the flood pulse but also by hydrologic disturbances that may reset these communities to earlier seral stages.

Low-order rivers are influenced by individual heavy rainstorms and show a spiky, unpredictable flood pattern of short floods that increase in frequency and in baseline flow during the rainy season (Fig. 1.2). Forests along streams and rivers play an important role by mitigating floods, trapping sediments, increasing bank stability, stripping nutrients from water and sediment, and providing food and habitat for animals and raw material for organic soils. They also filter nutrient input from the upland, enhance denitrification, equilibrate temperature, and control in-stream primary production by shading. Due to their linear arrangement, riparian forests are important corridors for genetic exchange between remote populations of aquatic and terrestrial organisms, mainly in unforested landscapes. Tree species diversity is high but species lists are rare, and the ecology of these wetlands has been poorly studied (Wantzen 2003; Wantzen et al. 2007). The small lateral extensions of these wetlands have resulted in a dramatic underestimation of the total area covered by them. Riparian forests along streams and low-order rivers in the rain forest are mapped as upland forests (*terra firme* forests). Junk (1993) estimated that, in Amazonia, they cover an area of about 1 million square kilometers. This corresponds to about 50% of the entire wetland area of the basin.

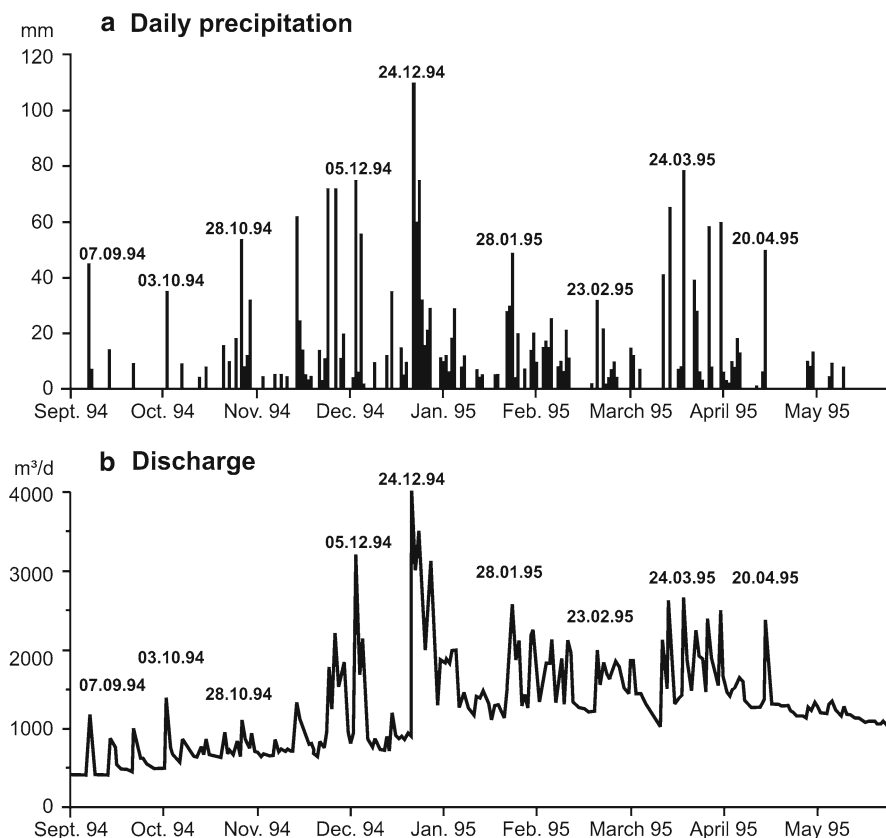
Because of the flat relief, drainage in large parts of the South American lowlands and plateaus is insufficient and leads to flooding due to excess rainfall. Periodic





**Fig. 1.1** Water-level fluctuations of the Negro/Amazon River at Manaus and the Paraguay River at Ladario (Data of the Amazon River from the Manaus harbor authority, of the Paraguay River from the Departamento Nacional de Águas e Energia Elétrica). ● = maxima; ○ = minima

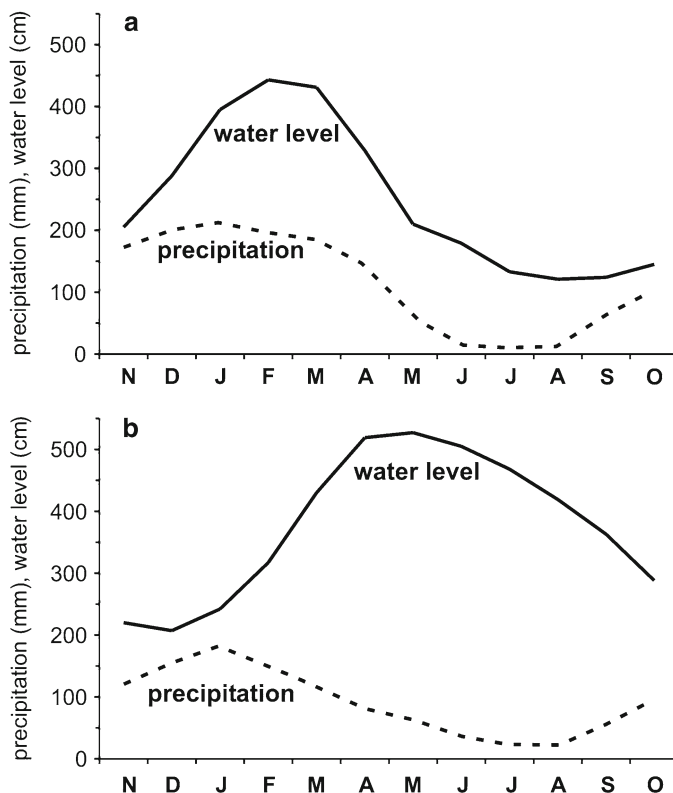
flooding and waterlogging of the soils during the rainy season has been reported from the Bana and Caatinga woodlands at the upper Negro and Orinoco Rivers, the Brazilian and Bolivian cerrado, the Argentinean chaco, and the Venezuelan savannah. These areas drain slowly to connected rivers. Isolated shallow lakes remain in depressions but can completely dry out during extreme dry periods. These floodplains show a long-lasting, predictable flood pulse of low amplitude (Fig. 1.3). In savannah areas, drought stress during the dry period can be intense. Nunes da Cunha and Junk (1999) reported that many tree species in the Pantanal of



**Fig. 1.2** Precipitation and discharge of the Tenente Amaral, at the study area a second order cerrado stream in Mato Grosso near Cuiabá (according to Wantzen 2003)

Poconé, upper Paraguay basin, are highly tolerant of drought and flood stress and that multi-annual periods of heavy drought and wild fires control the distribution of flood-adapted tree species, such as *Vochysia divergens*. Ishima (1998) showed that the increment in the diameter of *Vochysia divergens* is positively correlated with precipitation and restricted by drought stress but not by flood stress. Similar environmental conditions exist in the vast flooded savannas on Ilha do Bananal at the Tocantins River, in the Llanos dos Moxos at the Madre de Dios, Beni, Mamoré and Guaporé Rivers, in the flooded savannas of Roraima and Rupununi, and in the Llanos of Venezuela.

In the estuary, the tides impose a predictable polymodal flood pulse, with a moderate-amplitude effect on that of the Amazon River. This flood pulse affects the mangrove ecosystem but upriver also fresh water habitats. However, there have been no studies on the respective consequences.



**Fig. 1.3** (a) Mean monthly precipitation near Cuiabá (1933–1993) and mean water-level of the Cuiabá River at Cuiabá (1971–1988), northern Pantanal (According to Zeilhofer 1996). (b) Mean monthly precipitation near Corumbá (1912–1971) and mean water level of the Paraguay River at Ladário (1979–1987), southern Pantanal (According to Hamilton et al. 1999)

## 1.5 Geology and Paleoclimatology of Amazonia and the Evolution of Wetland Forests

The geologic and paleoclimatic history of Amazonia is closely related to water. The Amazon Basin is part of a very old depression that already existed in the Gondwana continent and then opened to the west. When South America separated from Africa, during the Early Cretaceous period, about 110 million years (Ma) before present (BP), the basin was already closed in the west by the Early Andes, except for an opening to the Pacific (Marañón Portal or Guayaquil Gap) that closed probably during the Late Cretaceous period (73 Ma). Rivers drained to the west into a depression along the eastern border of the Early Andes that opened to the Caribbean Sea. With the uplift of the Andes, the pre-Andean depression was subjected to marine incursions

in the Late Cretaceous (83–67 Ma), the Early Tertiary (61–60 Ma), and the Late Tertiary (11.8–10 Ma) periods, as indicated by marine sediments. Following the interruption of marine transgressions, the depression became covered by rivers, lakes, and extended wetlands. Large freshwater lakes were formed in the Tertiary period (Lago Pozo in the middle Eocene–early Oligocene, 43–30 Ma; and Lago Pebas in the Late Tertiary, 20–11.8 Ma) and were filled with sediments of riverine origin from the Andes and the shields of Central Brazil and the Guianas. In the Late Miocene (8 Ma), the connection to the Caribbean Sea and the Orinoco basin was closed by the Vaupes Arch. The Amazon River opened its way to the Atlantic Ocean by breaching the Purus Arch, and the modern Amazon drainage system incised large valleys and floodplains in the soft sediments (Lundberg et al. 1998).

This geologic history shows that the northeastern part of the South American continent was covered by extended saltwater, brackish water, freshwater lakes, and wetlands over long periods of time. Due to the region's position near the Equator, the climate was hot and humid. Differences between rainy and dry seasons led to water-level fluctuations in rivers and wetlands that in the larger of these took on a monomodal character, because of the large extension of the catchments. These environmental conditions favored the adaptations of plants and animals to periodic drought and flooding and thus to decreased extinction rates.

Paleobotanical evidence for the existence of extended tropical rain forests in South America is exceedingly rare and equivocal for the Cretaceous. In the Paleocene, the only evidence consists of a moderately high pollen diversity. For the Eocene, there are several lines of evidence for the existence of widespread, diverse rain forests taxonomically allied to modern neotropical rain forests (Burnham and Johnson 2004). Molecular-based phylogenies of several lineages of angiosperms, whose modern representatives are now largely restricted to tropical rain forests, indicate a Cenomanian origin (114–98 Ma) (Davis et al. 2002, 2004). They also suggest greater diversity among angiosperms in the Cretaceous, as evidenced by the few fossil records. The large number of fruit-feeding fishes and seed dispersal by fishes (ichthyochory) point to the co-evolution of floodplain forests and fishes. Fossils indicate that over the course of the last 13.5 million years or longer, fish such as tambaqui (*Colossoma macropomum*), which apparently has not changed its diet of fruits and seeds (Lundberg 1998; Lundberg et al. 1998), have persisted. Godoy et al. (1999) provided a preliminary list of 242 riparian tree species common to the Amazon and Orinoco River basin. These authors explained this high number by the past and present connectivity of river corridors.

The development of the extended floodplains along the lower and middle course of the Amazon River and its large tributaries was strongly influenced by a period of climatic changes during the Pleistocene. Several glacial periods led to drops in sea level up to 130 m, increased the declivity of the rivers, and led to deep erosions in the river valleys. This affected the lower courses of the tributaries of the Amazon River in the north and south, until the borders of the archaic shields, and the main stem in the west, up to 2,500 km inside the continent. During interglacial periods, the sea level rose and dammed the rivers back in their valleys. In the following millennia, the rivers filled their valleys with sediments, forming extended floodplains.

This process occurred rapidly in rivers transporting large amounts of sediments from the geologically young, uplifting Andes but slowly in rivers transporting small amounts of sediments from the old archaic shields and nutrient-poor tertiary freshwater sediments from Central Amazonia. Erosion and filling-in of river valleys took place several times, as can be shown by remnants of old river terraces along the Amazon River (paleo-floodplains) (Irion 1984a,b). The Andean zone is geologically very active because the Oceanic Nazca Plate continues to be pushed below the South American Plate. This movement results in uplifting and sinking sub-basins at the eastern pre-Andean zone, generating extended areas subject to periodic waterlogging or flooding (Räsänen 1993).

## 1.6 Classification of Amazonian Wetland Forests

The zonation of floodplain forests was described in early studies, e.g., by Takeuchi (1962) and Gessner (1968), but Keel and Prance (1979) were the first to provide figures on species distribution with respect to flood depth of an igapó forest of the Negro River, near Manaus. A first approach to classify Amazonian wetland forests according to hydrological and hydrochemical parameters was that of Prance (1979). One of the aims of that study was to define accurately the terminology used for the different types of wetland forests, because in the scientific literature the local terms *várzea* and *igapó* were used in different ways. Local people and many scientists applied the term *várzea* to all types of periodically flooded land (Ducke and Black 1953, 1954), whereas *igapó* was used to refer to permanently waterlogged swamp forest of the lower Amazon (Richards 1952). Other investigators included forests flooded by blackwater and whitewater under the term *igapó* (Gessner 1968; Moreira 1970).

Sioli (1956) correlated the hydrochemical conditions in Amazonian rivers with the geology and geomorphology of their catchment areas. Whitewater rivers, such as the Amazon main stem and the Purus, Juruá, and Madeira Rivers, have their origin in the Andes, from where they transport large amounts of nutrient-rich sediments. Their waters have a near-neutral pH and relatively high concentrations of dissolved solids, mainly, alkali-earth metals and carbonates. The electrical conductivity of the Amazon River decreases from about  $100 \mu\text{S cm}^{-1}$  near the Andes to about  $40 \mu\text{S cm}^{-1}$  at its lower course, by dilution with water from electrolyte-poor tributaries. Whitewater rivers deposit their sediments in large fringing floodplains, locally called *várzea*. These are fertile and covered with highly productive terrestrial and aquatic herbaceous plant communities and floodplain forests. Blackwater rivers, such as the Negro River, drain large areas of white sand into the central basin and on the shields. Their water is transparent with low amounts of suspended matter but high amounts of humic acids, which give the water a brownish-reddish color. The pH values are in the range of 4–5 and electrical conductivity is  $< 20 \mu\text{S cm}^{-1}$ . The floodplains of blackwater rivers are of low fertility and locally called *igapó*. They are covered by a slowly growing floodplain forest in which litter production is 30% lower (summarized in Furch and Junk 1997b) and the diameter-increment rates of trees is up to 50%

**Table 1.2** Key to the principle types of Amazonian forests subject to inundation (According to Prance 1979), a-d our modifications

Periodically inundated forest		
Flooded by regular annual cycles of rivers		
Whitewater	1	Seasonal várzea
Blackwater and clearwater	2	Seasonal igapó
Flooded by tidal movements		
Saltwater	3	Mangrove
Freshwater backup	4	Tidal várzea
Flooded by irregular rainfall (flash floods)	5	Floodplain forest <sup>a</sup>
Permanently inundated forest <sup>d</sup>		
Whitewater	6	Permanent swamp forest <sup>b</sup>
Blackwater and clearwater	7	Permanent Igapó <sup>c</sup>

<sup>a</sup>Riparian forests along low order rivers<sup>b</sup>Várzea swamp forest, várzea chavascal<sup>c</sup>Igapó swamp forest, igapó chavascal<sup>d</sup>Long-term inundated forests

lower than in várzea forest species. Terrestrial and aquatic herbaceous plants are scarce and many whitewater species are absent because of the low fertility and/or low pH (Junk and Piedade 1997). Clearwater rivers, such as the Tapajós, Xingu, and Tocantins Rivers, have their catchments in the archaic shields of Guiana and Central Brazil. Their waters are transparent and greenish, with low amounts of sediments and dissolved solids and an acidic pH that in large rivers varies between 5 and 6. Electrical conductivity in the large rivers is in the range of 20–40  $\mu\text{S cm}^{-1}$  but in low-order streams can decrease to 5  $\mu\text{S cm}^{-1}$ . The floodplains of clearwater rivers are of intermediate fertility and also called igapó.

Prance's floristic analysis of the different forest types (Prance 1979) supported the view of limnologists and led to the classification shown in Table 1.2.

Puhakka and Kalliola (1993), in their study of wetland forests in the Peruvian Amazon region, used river dynamics as the criterion to differentiate between two major groups: (1) vegetation in the meander zone of rivers, and (2) swamp vegetation in flooded lowlands. The first group is characterized by highly dynamic erosion and sedimentation processes leading to different arrangements of successional stages of herbaceous and forest communities. The second group covers poorly drained, geomorphologically rather stable areas in abandoned floodplains with relatively stable vegetation types that are considered to be in climax (herbaceous swamps, shrub swamps, palm swamps, and forested swamps).

Kubitzki (1989a,b,c) followed the classification of Prance and explained the floristic differences between várzea and igapó as arising from differences in nutrient status. He also pointed to the close floristic ties between floodplain forests and forests in the adjacent uplands (terra firme). Especially close relationships exist between terra firme forests on latosols and várzea forests. Many upland species have developed flood-tolerant ecotypes in the várzea, e.g., *Guazuma ulmifolia* and *Spondias lutea*. The genus *Maquira* (Moraceae) has one species in the várzea (*M. coriacea*),

another occurs there facultatively (*M. calophylla*), and others are restricted to the terra firme (Berg 1972). In the western part of the Amazon rain forest, many várzea species also occur on terra firme, e.g., *Ceiba pentandra* and *Pseudobombax munguba*, because of the better nutrient status of terra firme soils near the Andes.

The flora of the igapós has close connections with the woodlands of oligotrophic campinas and caatingas and with those of white-sand savannahs. These areas show periodically high groundwater levels or even shallow flooding and thus require the respective adaptations by trees. Many of these species, such as *Qualea retusa*, *Panopsis rubescens*, and *Humira balsamifera*, are also found in the upper parts of igapós. In some genera, all species are restricted to periodically flooded habitats, such as *Ramatuella*, *Haploclathra*, *Leopoldinia*, *Glandonia*, *Pachira*, and *Lophantera* (Kubitzki 1989).

Many species reside in várzea and igapó, among others, *Campsiandra laurifolia*, *Macrolobium acaciifolium*, *Symmeria paniculata*, *Virola elongata*, *Caryocar microcarpum*, *Allantoma lineata*, *Caraipa densifolia*, *Pachira aquatica*, *P. insignis*, *Swarzia polyphylla*, and *Vatairea guianensis* (Ducke 1913; Prance 1979; Kubitzki 1989; Wittmann et al. 2010).

Centers of endemism of floodplain tree species are located in the upper Negro River basin, including the Rio Negro Refuge (Steyermark 1982), the Amazonas Savannahs Refuge (Huber 1982) and parts of the Imeri Refuge of Prance (1973). Endemic to this area are: *Leopoldinia piassaba*, *L. maior*, *Mauritia carana*, *Mauritiella aculeate*, *Schistostemon oblongifolium*, the genus *Ramatuella*, *Ocotea esmeraldana*, *Glandonia williamsii*, *Asteranthus brasiliensis*, *Henriquezia nitida*, *Vitex calothyrsa*, and several species of *Swartzia* and *Macrolobium* (Kubitzki 1989).

We agree with Prance's use of hydrological and hydrochemical parameters to classify wetland forest. However, we consider the term "floodplain forest" of type 5 inadequate, because "floodplain forest" is a general term that can be used for types 1–5, all of which occur on different types of floodplains, in contrast to types 6 and 7, which occur on permanently waterlogged habitats. Forest type 5 flooded by irregular rainfall (flash floods) is a riparian forest along low order rivers and we use this more specific term. All Amazonian flooded forests have to fall dry at least for rejuvenation. Therefore we use the term "long-term inundated forests" instead of "permanently inundated forests". We also consider it inappropriate to denominate várzea swamp forests (type 6) as "permanent swamp forest." Swamp forest is a general category that describes all types of forests on long-term-flooded or waterlogged habitats. Várzea swamp forest and igapó swamp forest correctly describe their respective types according to flooding regime and nutrient status. Locally, these forests are denominated *chavascal*. Ayres (1993) described the *chavascal* of the Mamirauá Reserve for Sustainable Management, near Tefé, as swampy shrub vegetation with a few higher trees that is nearly impenetrable for humans at low water. It is flooded for 6–8 months per year to a depth of 6–7 m. According to Wittmann et al. (2004), the *chavascal* is established in poorly drained depressions with waterlogged soils, which leads to an accumulation of organic material. We use this term for this vegetation type as well. To characterize nutrient status, we differentiate between the nutrient-rich várzea *chavascal* and nutrient-poor igapó *chavascal*.



## 1.7 Flood Tolerance and Adaptations for Survival during Periodic Flooding

Flood tolerance is the capacity of higher plants to survive flooding by the development of:

- Anatomical structures, e.g., gas transport systems, which facilitate gaseous diffusion from the shoot to the root
- Morphological structures to cope with periodic flooding (stilt roots, tabular roots)
- Metabolic adaptations to anoxic environments (Crawford 1969)

For most plant species, periodic flooding results in stress. Stress describes external constraints limiting resource acquisition, growth, or the reproduction of an organism (Grime 1989). For plants, the primary constraint imposed by flooding is impeded gas exchange. The diffusive resistance of most gases in water is about 10,000 times greater than in air. There is also a 30-fold drop in oxygen concentration between the gaseous and the dissolved states. In the tropics, oxygen deficiency is pronounced because with increasing temperature the solubility of oxygen in water decreases from about 14.2 mg l<sup>-1</sup> at 0°C to about 7.0 mg l<sup>-1</sup> at 35°C. At the same time, microbial oxygen demand increases with increasing temperature and quickly leads, in waterlogged soils, to anoxia, a negative redox-potential, and the mobilization and production of substances potentially detrimental to plant roots, such as dissolved iron and manganese, and H<sub>2</sub>S (Piedade et al. 2010).

Oxygen stress in roots is accompanied by a decline in energy levels, a more rapid depletion of carbohydrate reserves, changes in cytoplasmic pH, and ultra-structural alterations. Deep flooding lengthens the diffusion path for gas transport and may reach the photosynthetically active parts of the plant, thereby interrupting CO<sub>2</sub> assimilation and respiratory oxygen supply, and decreasing light availability for photosynthesis.

Plants have developed different structural and metabolic strategies, often linked to the growth cycle and to reproductive strategies, to cope with these conditions (Blom 1990; Voesenek et al. 1992). These strategies include: (1) efficient gas transport, for instance, by surface rooting, diffusion through the gas-space system, formation of aerenchymatic tissue, connective gas flows, and controlled radial oxygen loss to the rhizosphere; (2) metabolic adaptations, such as the control of energy metabolism under oxygen deprivation, the availability of extensive energy resources, the provision of essential gene products, macromolecular synthesis, and protection against post-anoxic injury (Hendry and Brocklebank 1985). Furthermore, there is some evidence linking flooding to hormone-triggered changes in morphology (e.g., the hormones ETH, IAA, GA, CK, and ABA), such as root extension, aerenchyma formation, promotion of shoot extension, stem hypertrophy, and adventitious rooting (Armstrong et al. 1994).

In Amazonia, the first studies on the flooding-tolerance of trees were carried out by Gessner (1968), Scholander and Perez (1968), Joly and Crawford (1982),

and Schlüter (1989). Joly (1991) correctly pointed out that in the majority of cases a successful strategy to survive periodic flooding is a combination of morphological, anatomical, and metabolic adaptations. The results of recent studies are discussed in Piedade et al. and Ferreira et al. (2010).

### 1.8    Determination of Flooding Tolerance in the Field

The efficiency of a given strategy – or a combination of strategies – against flooding or water-logging of the soil defines the flooding tolerance of a species or its ecotypes. Adaptations in the growth cycle and reproductive strategies determine whether a species can establish viable populations in wetlands and which position it occupies along the flooding gradient in a river floodplain. There is no sharp borderline between flood-tolerant and flood-intolerant species, which makes comparative studies, e.g., on tree species diversity in river floodplains, very difficult.

Ecologists consider all tree species that occur in river floodplains as flood-tolerant, because they assume that these trees have survived many flood periods during their life histories. The length of the flood period is an important parameter in quantifying flood tolerance, as shown for some shrubs and trees of the Rhine River floodplain (Table 1.3). However, the total number of flood days may be misleading, when the timing and frequency of the flood events are not given as well. In temperate regions, floods in late autumn, winter, and early spring have little effect on the trees because they are in a physiological resting stage, whereas the effects in late spring, summer, and early autumn are large because at those times the trees are fully active. Furthermore, flood stress for trees growing in a gallery forest of a small river subject to several short flood pulses for 60 days of flooding per year differs from that in a floodplain of a large river subjected to a single flood event of 60 days per year.

**Table 1.3** Flooding tolerance of tree species of the Rhine River floodplain. Data are given for trees on the lowest-lying habitats during a 10 year period (Dister 1983)

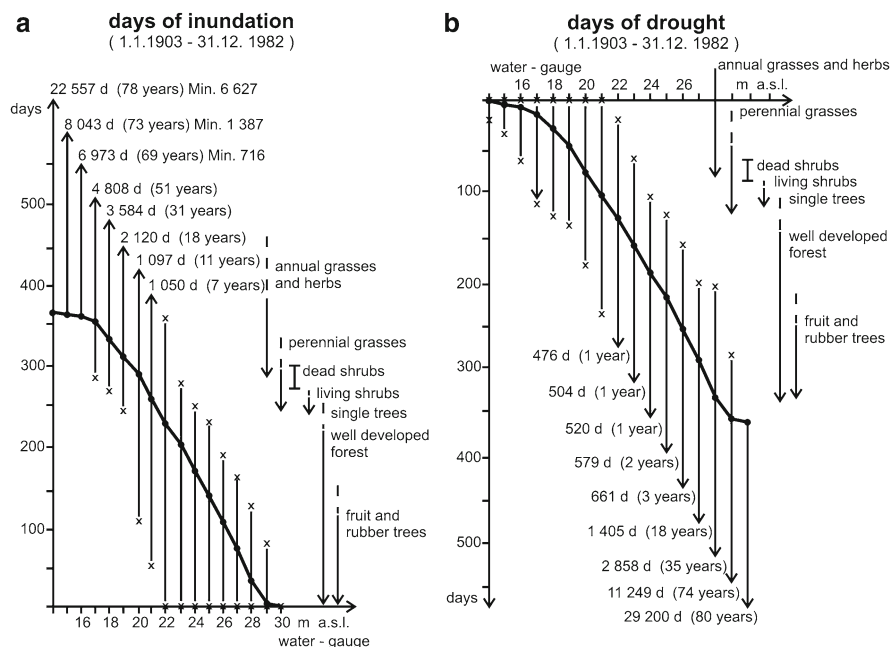
Species	Length of inundation (days) <sup>a</sup>		Depth (m)
	Minimum	Maximum	
<i>Salix alba</i>	190	300	4.80
<i>Ulmus minor</i> , <i>U. laevis</i>	100		
<i>Quercus robur</i>	97	217	4.25
<i>Crataegus monogyna</i>	40	120	
<i>Fraxinus excelsior</i>	40	102	
<i>Acer pseudoplatanus</i>	8	35	
<i>Corylus avellana</i>	3.5	22	

<sup>a</sup>20–50% of the inundation days fall in the period of low physiological activity

In their natural habitat, trees are distributed along a flooding gradient in a characteristic pattern that is determined by abiotic and biotic factors. Abiotic factors are length, depth, frequency, timing and shape of the flood pulse, current velocity, sedimentation rate, sediment quality, erosion, drought stress at the low-water period, and, in temperate regions, ice damage. Biotic factors are competition, organic-matter content and related oxygen concentrations in soils, seed dispersal, and seedling establishment. Large trees survive floods better than small trees, because flood length is often correlated with flood depth, and many trees cannot tolerate total flooding during the growth period. Trees distributed in the lower ranges of the flooding gradient rejuvenate only in years of very low flood levels (Oliveira Wittmann et al. 2010). However, the growth form of the species can also influence its position on the flooding gradient. In the Rhine River floodplain, the shrubby *Salix purpurea* grows on a higher position than the tree *Salix alba*, not because of lower flood tolerance but to avoid total flooding (Dister 1983). Some floodplain species, such as *Salix* spp. and *Populus* spp. in temperate regions, and *Salix humboldtiana*, *Alchornea castaneifolia*, and *Pseudobombax munguba* in the Amazon várzea, require vegetation-free sediments for germination and seedling establishment. Little-disturbed habitats that are quickly occupied by fast-growing herbaceous plants hinder seedling establishment by these tree species due to shading, despite a tolerable flood stress.

In the humid tropics soil saturation with water and following short anoxic conditions because of high microbial activity under high temperature may occur frequently after heavy rains in many habitats that are not considered wetlands. These conditions may favor a predisposition for flood tolerance in many tropical rain forest species, as shown by Lopez and Kursar (1999, 2003). Frequent short floods in gallery forests along small streams and in depressions select for flood tolerance. The flooding of large, rain-water-fed interfluvial floodplains can last many months but is shallower than that of large-river floodplains, such as the várzeas and igapós of the middle Amazon and its tributaries, where flooding in the low-lying parts is long-lasting and up to 15 m deep. This sequence is reflected by the difference between high-várzea and-low várzea forests and their relationships to the non-flooded upland forest (Wittmann et al. 2010).

The distribution of plant communities along the flooding gradient of the middle Amazon River and information regarding the length of the flood period was provided by Junk (1989). As seen in Figure 1.4, the lowest part of the flooding gradient is covered by short-lived annual grasses, sedges, and herbaceous plants that build a flood-resistant seed bank in the sediment. Higher up on the gradient, perennial aquatic grasses are established that have their growth period during high water and re-establish their populations vegetatively or by seeds during low water (*Echinochloa polystachya*, *Paspalum repens*). Other species have their growth period during the low-water season, survive flooding with flood-resistant stems, and vegetatively re-establish their populations during the low-water season (*Paspalum fasciculatum*). These vigorously growing grasses occupy a position on the flooding gradient that can also be occupied by trees. They suppress, often for many years, sapling establishment by intense competition for light. Flood-resistant shrubs



**Fig. 1.4** Distribution of major terrestrial plant communities on the flood-level gradient of the Amazon River floodplain near Manaus. The data are based on the 80-year average maximum and minimum numbers of consecutive dry and flood days (hydrological data from Manaus harbor). Totals of the number of years without dry and flood periods are indicated in parentheses. Values are calculated according to the hydrological year (Junk 1989)

(*Cocoloba ovata*, *Symmeria paniculata*, *Eugenia inundata*) grow on habitats that are inundated during nearly 9 months per year on average, but can tolerate extreme periods of 3 years of consecutive flooding of the rhizosphere. A species-rich floodplain forest establishes on areas flooded on average during 8 months of the year or less, but single specimens on low-lying areas can also tolerate flooding during two consecutive years. Near Manaus, Igapó forests colonize areas about 1 m lower on the flooding gradient, probably because water is not anoxic near the bottom. The flood tolerance of certain fruit trees, such as mango, bread fruit, and coconut, is economically important. Based on the high species diversity of Amazonian floodplain forests, we postulate that the diversity and complexity of strategies that have evolved to deal with flooding are much higher than in floodplain forests of temperate regions (Wittmann et al. 2010).

To what extent periodic flooding is a pre-requisite for the growth of floodplain trees is an open question. In most tree species, wood increment increases with increasing length of the terrestrial phase. Our preliminary experiments, in which floodplain trees were planted in non-flooded areas, showed positive results when saplings, during the first years, received additional fertilization and were protected

against competition from other species and from the attack of herbivorous insects. This observation points to a competitive disadvantage of these species against terra firme species. Growth of *Vochysia divergens*, a flood-tolerant tree species from the Pantanal of Mato Grosso, is correlated with rainfall, implying that water shortage may be a limiting factor. These assumptions have been corroborated by the observation that many species of the high várzea forest in western Amazonia also occur on non-flooded habitats with better nutrient supply and high rainfall (Kubitzki 1989).

The seed-dispersal strategies of many species illustrate the importance of water for the maintenance of viable populations. Many species, such as *Panopsis rubescens*, *Swartzia polyphylla*, *Cynometra spruceana*, *Glandonia* spp., and *Burdachia prismatocarpa*, have developed floating fruits or seeds to facilitate dispersal by water (Kubitzki 1989, Parolin et al. 2010b). Others species of seeds are distributed by fishes, e.g., *Bactris* sp., *Calyptanthes ruizana*, *Pseudoxandra* sp., *Genipa americana*, *Byrsonima* sp., *Mouriri* sp., *Endlicheria* sp., *Tetragastris unifoliata*, and *Quina rhythidopus* (Goulding 1980).

## 1.9 The Use of Amazonian Floodplain Forests

With up to 28 (mean 14.6) persons per square kilometer, Amazonian whitewater river floodplains were densely colonized already in pre-Columbian times (Denevan 1976). However, we may assume that the impact on the várzea forest was relatively small, because there was little demand for wood and arable land, and there was no need to increase pasture area because large-scale animal ranching was not known. Forest destruction started in the middle of the nineteenth century with the enormous demand for wood to fuel the engines of steamships. Agriculture and cattle ranching started on a small scale around Belem and Manaus, but at the beginning of the twentieth century spread from Belem up-river. In 1929, jute cultivation for fiber production began near the city of Parintins and reached 25,000 t in 1953. By the time the boom had started to decline in the 1970s, because of competition from plastic sacks and cheap fiber from Bangladesh, large areas of the lower Amazon River floodplain had already been deforested (Gentil 1988; Goulding et al. 1996).

Selective logging decreased the stocks of a few preferred timber species of medium to high wood density that were later substituted by others (Schöngart, Schöngart et al. 2010a). These were exploited in the same unsustainable manner, i.e., first the forests near urban centers and later also those in remote areas were degraded. For the last several decades, softwood species, such as *Ceiba pentandra*, have been heavily exploited for plywood production. Previously very common in the várzea, this species is now rare with very little regrowth. Selective logging reached the Amazon tributaries in the 1980s, after most floodplain forests along the main river had been selectively logged. Today, most wood used in cities along the Amazon River still comes from the floodplains of the upper Solimões, Madeira,

and Purus Rivers, but commercially exploitable forest resources are nearly depleted. During the entire period of forest exploitation, there has been very little regrowth because, with increasing agriculture and cattle ranching, high várzeas were deforested. These areas provided fertile soils for sufficiently long dry periods of crop and pasture plantations. Today, most floodplain forests on the lower Amazon River are species-poor secondary forests, and the few remnant mature forests are heavily degraded. Nearly pristine forests still remain in Brazil at the middle Solimões, mainly in the Sustainable Management Reserve of Mamirauá, near the city of Tefé.

Today, the heavy pressure exerted by farmers, cattle ranchers, and logging companies on the forests continues, and management concepts are urgently required to avoid the destruction of this unique forest type. The várzea is one of the very few sites in central Amazonia where the nutrient stock in the alluvial soils is replenished by the annual floods and is sufficiently high to allow the sustainable production of timber and non-timber products (Furch 1997, 2000). Several native floodplain tree species show fast growth rates and are of interest for the timber market. They provide economically viable and ecologically sound options for the local inhabitants as well as the timber industry (Wittmann and Oliveira Wittmann 2010). Other services of the floodplain forests, such as river-current breakers, protection of the floodplain against erosion, carbon sink, habitat and food source of many animals including economically important fish species, gene pool of flood-tolerant species or ecotypes, etc., are of major importance for humans and the ecosystem, but are little acknowledged by planners.

Technical assistance for várzea forest management cannot be expected from forestry in the Amazonian terra firme, which to a large extent is restricted to non-sustainable timber extraction, frequently followed by transformation of the plots to pasture or soybean plantations. Only a few enterprises are attempting to manage upland forests sustainably. However, the management methods of these forests cannot be applied to várzea forests, because the environmental conditions in floodplains are quite different. Instead, specific management systems for floodplain forests are required (Schöngart 2010). A fundamental deficiency of management concepts in most tropical rain forests is the lack of precise information about the growth rates of individual trees in the stands. The small differences in rainfall between the dry and rainy seasons lead to the barely pronounced formation of annual rings in many Central Amazonian terra firme tree species, which makes the determination of aging by tree-ring analysis difficult. In várzea and igapó, the heavy stress of prolonged deep flooding leads to a reduction of diameter increment and the formation of well-developed growth rings in many tree species, even in those that do not shed their leaves and that are photosynthetically active during the flood period. The development of a methodology to determine individual growth rates and wood production by tree-ring analysis is a pre-requisite for the establishment of growth models of different tree species and the basis of management concepts (Worbes 1984, 1989; Worbes and Junk 1989). It will allow the sustainable use of floodplain forests by protecting their species diversity along with the other benefits of these ecosystems (Worbes and Fichtler 2010).

## 1.10 Discussion and Conclusions

Inventories indicate that Amazonian floodplain forests are the most diverse wetland forests worldwide, containing more than 1,000 tree species (Wittmann et al. 2006a). Geological evidence supports the existence of extended wetlands since the Early Cretaceous period, when South America separated from Africa. Furthermore, the position of the Amazon River basin near the Equator provided relatively high paleoclimatic stability. These conditions favored the development of adaptations by trees to periodic flooding and diminished the risk of species extinction during adverse periods.

Different types of wetlands cover large areas of tropical and sub-tropical South America. In all of them, flood-tolerant trees play an important role in the vegetation cover. Individual trees and forest patches occur in flooded savannas, while strips of riparian forests accompany savannah and forest streams, and mangroves grow on the coastline. About one million square kilometers, corresponding to 14% of the Amazon basin, are covered by wetland forests. A major portion of these forests is located in narrow strips along low-order streams and rivers. Extended swamp forests are found in interfluvial areas in the Amazonian lowlands. Of great economic importance are the floodplain forests along the Amazon River and its large whitewater, clearwater, and blackwater tributaries, the várzea, and igapó. These cover an area of about 400,000 km<sup>2</sup> (Junk 1997b). Várzea forests are under particularly heavy human pressure, since most of the timber used in urban centers along the Amazon River is logged in these forests. Fertile alluvial soils in the várzea attract farmers and cattle-ranchers, who destroy the forest for crop and pasture plantations. Today, floodplain forests along the lower Amazon River are heavily degraded, and selective logging has modified species composition along most of the river's tributaries. In Brazil, major areas of nearly pristine várzea forests still exist in the Reserve for Sustainable Management of Mamirauá, at the confluence of the Japurá and Solimões Rivers.

Despite the economic and ecological significance of Amazonian large-river floodplain forests, ecological knowledge is limited. Until the 1970s, studies in the Amazonian floodplain forests were mostly carried out by botanists, who provided the taxonomic basis for further research (Ducke and Black 1953, 1954; Takeuchi 1962; Pires 1961; and others). In the following years, several studies greatly improved our understanding of floodplain forests. Prance (1979) classified wetland forest types according to hydrological, chemical, and floristic parameters. His classification was in agreement with that of limnologists (Sioli 1956; Irmiler 1977) and ended terminological confusion in the scientific literature. Floristic studies in the pre-Andean zone called attention to the importance of river dynamics in the development and maintenance of Amazonian biodiversity (Salo et al. 1986). Junk (1989) was the first to quantify flood stress by correlating the length and depth of flooding with the occurrence of plant species and communities in the várzea. Kubitzki (1989) showed the floristic relationship of várzea forests to nutrient-rich terra firme forests on latosols in eastern Amazonia and of igapó forests to oligotrophic terra firme woodlands of campinas, caatingas, and white-sand savannas.



Of fundamental importance for productivity studies was the description of annual growth rings in floodplain tree species (Worbes 1984; Worbes and Junk 1989). It allowed calculation of the wood increment of individual trees and established the basis for the first sustainable management concept of tropical rain forests, based on individual growth rates over the entire life span of the trees. These studies presented the basis for a period of intensive research in the Central Amazon River floodplain by a team of Brazilian and German scientists in the frame of a cooperation treaty between CNPq, on the Brazilian side, and the Max-Planck-Society and BMBF (during 12 years) on the German side. The work was carried out by investigators at the INPA (Manaus) and MPIL (Plön).

The results of these studies and the remote sensing data obtained by a team of scientists at the University of Santa Barbara, California, are presented in this book and provide a synopsis of the current state of knowledge concerning the ecophysiology, primary production, biodiversity, and sustainable management of Central Amazonian floodplain forests.